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Old female reed buntings (*Emberiza schoeniclus*) increase extra-pair paternity in their broods when mated to young males

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Summary

In birds, females are generally assumed to determine whether extra-pair copulations occur, and thus most studies on extra-pair paternity (EPP) have focussed on female preference for male traits, whereas female traits have been largely neglected. However, the occurrence of EPP is likely to be a result of behavioural interactions (e.g., mate guarding by the social male and escaping mate guarding by the female), and may be related to individual experience, which is expected to increase with age. We investigated the effect of age on levels of EPP in reed buntings *Emberiza schoeniclus*, a socially monogamous passerine with extremely high levels of extra-pair young (more than 50% of offspring). In broods of older males the rate of cuckoldry declined, which is in agreement with our previous finding that older males are more successful, either through female choice or through male experience. In contrast, older females tended to increase the level of extra-pair paternity in their broods. When including the age of the partner, we found that young males, but not old males, were cuckolded more by old females than by young females. The increase in EPP with female age is not likely to be due to disassortative mating with respect to age, an increased capacity of older females to raise a brood without male help, nor a male preference for older females. With age, males nor females changed their share in parental effort. We suggest that with increase in age, females become more choosy when selecting the male that sires their offspring, or alternatively, become more experienced at circumventing paternity assurance tactics of young males.

Keywords: extra-pair paternity, age, pair combination, *Emberiza schoeniclus*.

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Introduction

Extra-pair paternity (EPP) has been the focus of many studies of socially monogamous birds (Griffith et al., 2002). By gaining extra-pair fertilisations (EPFs), males may increase their reproductive success, while the expected benefits to females are more controversial (Birkhead & Møller, 1992). With the absence of a male intromittant organ in most bird species, female active participation in copulation is generally required for insemination to be successful (Birkhead & Møller, 1992). Extra-pair copulations (EPCs) are likely to be costly to the female, since males are expected to provide less care to offspring sired by other males (Trivers, 1972), giving rise to conflicts over parental investment. Thus, females are only expected to engage in EPCs if there are potential benefits (Westneat et al., 1990; Birkhead & Møller, 1992). Indeed, evidence has been found that females actively pursue EPCs in some bird species (e.g., Smith, 1988; Kempenaers et al., 1992; Double & Cockburn, 2000). Moreover, the likelihood of EPCs resulting in extra-pair offspring may be influenced by females, e.g., by careful timing of the EPCs and within-pair copulations around egg-laying (Sheldon, 1994; Gray, 1997) or e.g., by resisting certain intruder males as extra-pair males (e.g., Heg et al., 1993; Dickinson, 2001). Most widespread support has been found for females gaining genetic benefits for their offspring through extra-pair matings, but the results are not consistent in all studied species (Foerster et al., 2003; Schmoll et al., 2003; Kleven & Lifjeld, 2004; reviewed by Griffith et al., 2002).

Many studies have found that male characteristics, such as plumage coloration, song, but most commonly age, are related to fertilisation success (reviewed by Griffith et al., 2002). This non-random distribution may be a result of two, not mutually exclusive, mechanisms: (i) females may actively choose good viability genes of older males for their offspring (Richardson & Burke, 1999), or (ii) older males increase their experience or investment in protecting paternity in their own brood and gaining paternity in other broods (Weatherhead & Boag, 1995). Due to the increased risk of cuckoldry, younger males have been found to mate guard more intensively than older males in several species (e.g., Wagner et al., 1996; Johnsen et al., 2003). However, this does not necessarily translate into higher levels of paternity, indicating that females can circumvent these paternity guards.

As individuals are often found to enjoy increased breeding success with greater experience (Clutton-Brock, 1988; Saether, 1990), possibly females

also increase successful extra-pair mating behaviour with greater experience and thus age. However, the relation between female characteristics and EPP has received far less attention so far than the relationship between male characteristics and EPP (but see Westneat, 1992; Dunn et al., 1994; Wagner et al., 1996; Stutchbury et al., 1997; Cordero et al., 1999; Kempenaers et al., 1999; Weatherhead, 1999; Li & Brown, 2000; Veiga & Boto, 2000; Dickinson, 2001). Only three studies have reported female age to be correlated with the proportion of EPP in their broods. Young female hooded warblers, *Wilsonia citrina*, had higher levels of EPP in their broods; they arrived later on the breeding site than older females, possibly restricting them in their choice of social mates (Stutchbury et al., 1997). As a consequence, young females may be forced to pair with low quality social males and therefore seek more EPPs than females mated to high quality males (Westneat et al., 1990). In contrast, old female tree swallows, *Tachycineta bicolor*, and coal tits, *Parus ater*, were more likely to have higher levels of EPP in their broods compared to young females (Kempenaers et al., 1999; Dietrich et al., 2004). However, in coal tits, this appeared only to be the case when females were paired to young males, but not when paired to old males, which suggests an interaction between the ability of males to mate guard on the one hand and of females to escape mate guarding on the other (Dietrich et al., 2004). The occurrence of EPP is thus not likely to be a result of only the female deciding whether or not to engage in extra-pair copulations, but of the interaction between the female, social male and extra-pair male and this interaction deserves more attention in behavioural studies than received so far (Westneat & Stewart, 2003).

We investigated levels of within brood EPP in relation to age of the social parents in the reed bunting *Emberiza schoeniclus*, a socially monogamous passerine with very high rates of EPP (55% of offspring, Dixon et al., 1994; 50% of offspring, Bouwman et al., 2005). We previously found that older males were more successful than younger males in siring offspring outside their own brood and tended to be more successful in siring offspring within their own brood (Bouwman et al., in press b). Assuming that females actively seek EPCs and gain experience in extra-pair mating behaviour with age, we expected the proportion of EPP in the broods of individual females to increase from one year to the next. More specifically, when including the age of the partner, we expected to find a pattern similar to the one observed in coal tits (Dietrich et al., 2004). As old males are most successful in siring

offspring, we expected both young and old females paired to old males to have low levels of EPP in their broods. Since old females are expected to be more experienced in escaping mate guarding, we predicted old females paired to young males to have higher levels of EPP in their broods. Not only experience in escaping mate guarding behaviour may increase with age, but also individual quality measures and breeding experience, thereby potentially influencing the costs and benefits of engaging in extra-pair mating behaviour. We assessed whether, with age, reed buntings increased their adult mass, onset of breeding, clutch size of the first brood, hatching and fledging success and share of nestling food provisioning rates, thereby influencing possible costs and benefits of having EPP.

Methods

General

We studied a population of reed buntings in 2002 and 2003 in a 13 ha study site, on the small island of Noorderplaat (45 ha) in 'De Biesbosch' National Park in the Netherlands (51°45'N, 4°45'E). Adults were caught using mist-nets, individually colour-ringed, blood sampled and weighed. Forty-four and 35 pairs bred in our study area in 2002 and 2003, respectively. In 2002, we ringed 97% of all individuals ($N = 88$) within the main study area (i.e., the area where we attempted to find all nests) and 80% of individuals ($N = 20$) from surrounding territories. Forty-two percent of ringed adults breeding in 2002 returned to our study area the following breeding season and all reoccupied the same or a nearby territory. As recruitment rates of fledglings are very low and adult reed buntings cannot be reliably aged using plumage characteristics, few adults were of exact known age. We assumed ringed adults returning in 2003 to be 'old' breeders ($N = 37$) and unringed adults to be 'young' breeders ($N = 41$; Veiga, 1993; Yezerinac & Weatherhead, 1997). In support of our assumption, we found that wing length increased for most individuals from one year to the next ($p < 0.001$) and, in agreement, 'young breeders' had significantly shorter wings than 'old' breeders ($p < 0.001$; Bouwman et al., in press b).

Nests were located through systematic searches that flushed females off the nest, or by checking territories for any nest-related activities. The identities of the male and female belonging to a nest were determined by direct

observations of colour-ringed birds protecting the nest, or video recordings of birds incubating and feeding nestlings. Blood samples of nestlings were taken two days after hatching. Unhatched eggs were removed and inspected for embryonic development, which was used as a source of DNA. Video recordings (3 hours) were made of adults feeding nestlings when the oldest nestling was between 4 and 6 days of age.

Paternity analysis

DNA was extracted from blood samples using salt extraction (Richardson et al., 2001). Individuals were genotyped using six fluorescently labelled microsatellite markers: *Escμ1*, *Escμ4*, *Escμ6* (Hanotte et al., 1994), *Pdoμ5* (Griffith et al., 1999), *Mcyμ4* (Double et al., 1997) and *Ppi2* (Martinez et al., 1999). For a detailed description of the methods see Bouwman et al. (in press a). Parentage was determined by using a likelihood-based approach in CERVUS (version 2.0; Marshall et al., 1998). This program assesses the confidence of paternity exclusion using criteria generated through a simulation taking into account allele frequencies in the population, the number of possible candidate parents, the proportion of candidate parents sampled, and the percentage of missing genetic data and genotyping errors. CERVUS was given the choice between two candidate parents: the social male and one potential, but unknown, extra-pair male. The program calculates the likelihood that the social male is the actual father by using the natural logarithm of the likelihood ratio or so called LOD score. The social male is assigned as the father if the LOD-score is positive and rejected if the LOD-score is zero or below. To accept the male as the father, a critical difference is required in LOD scores between the first and the second candidate. The critical values were calculated by entering the following simulation parameters in CERVUS: 2 candidate parents and 50% of candidate parents sampled. Assigned males were accepted at >95% confidence. None of the loci deviated significantly from Hardy-Weinberg equilibrium. Using the observed allele frequencies, CERVUS calculated a total exclusionary power for the six microsatellite loci; in both years the probability of exclusion was 0.993 for assigning the father when the mother is unknown ('first parent') and 0.999 for assigning the father when the mother is known ('second parent').

Data analysis

First, we determined the proportion of EPP from one year to the next within individuals. We used 15 males and 9 females that produced at least one brood with known paternity in both 2002 and 2003. Only one pair from 2002 remated in 2003. This pair was included in the analysis and highlighted in the figure. If within a year more than one brood was sampled per pair, we averaged the levels of EPP. The level of EPP was arcsin transformed to attain a normal distribution, after which a paired *t*-test was used.

Second, we determined the proportion of EPP in relation to age across individuals. As we could only distinguish between 'young' (unringed) and 'old' (colour-ringed in 2002) breeders in 2003, we used 30 pairs breeding in 2003 to determine the effect of age (i.e., young vs old) and the interaction between male and female age on EPP. We used multilevel generalized linear mixed models to analyse the effect of age on the proportion of EPP in a brood, assuming a binomial error distribution with logit-link function and using the number of offspring in a brood as the denominator. The two-level hierarchical structure of the proportional response data was built up with the identity of the pair as the highest level and the different broods for each pair as the lowest level (i.e., one or two broods). This approach allowed us to make full use of all available broods, while accounting for more than one brood per pair. The model was estimated using reweighted iterative generalised least squares (RIGLS) and 2nd order penalised quasi-likelihood approximation (PQL; Rasbash et al., 2004). The significance of variables was tested using the Wald statistic, which follows a χ^2 -distribution.

We investigated the relationship between the proportion of EPP in broods of individuals in 2002 and their probability of returning to our study site in 2003 by using multilevel generalized linear mixed models, again assuming a binomial error distribution with logit-link function and using the number of offspring in a brood as the denominator. The two-level hierarchical structure of the proportion of EPP was built up with the identity of the male or female as the highest level and the different broods for each individual as the lowest level.

On average first clutches were initiated five days earlier in 2003 than in 2002 (day 1 = 1 April; 2002: day 41 (range: 22-87); 2003: day 36 (range: 28-76)). The first egg day for an individual was corrected for year-effect by subtracting the average first egg day for that year. Fledging success was

not comparable within individuals between years, as predation rates differed between years. The probability of nest predation did not depend on the age of the social male ($\chi^2 = 0.08$, $p = 0.77$) or female ($\chi^2 < 0.01$, $p = 0.97$). Statistical analyses were performed using SPSS 11.0.1 (SPSS Inc.) and MLwiN 2.0. Non-parametric tests were used if data were not normally distributed after transformation. Probability values are two-tailed and means are presented with standard errors (SE).

Results

Extra-pair males sired 54.6% of offspring in 2002 ($N = 262$) and 46.4% of offspring in 2003 ($N = 211$; Bouwman et al., in press a). The proportion of EPP in a male's brood declined as he aged one year (Figure 1a), while females tended to have a higher proportion of EPP in their brood when they grew one year older (Figure 1b). After combining male and female age and their interaction in one model, we found a significant negative effect of the interaction between male and female age on the proportion of EPP in a brood (Table 1). When comparing the proportion of EPP for each age combination of the social parents (Figure 2), we found that old females paired to young males had a near significant higher proportion of EPP in their broods than when they were paired to old males (Wald = 3.62, $df = 1$, $p = 0.057$). We also found that the combination old females paired to young males tended to have a higher proportion of EPP than young females paired to young males (Wald = 3.42, $df = 1$, $p = 0.064$). The proportion of EPP did not differ between pairs of young females and either young or old males (Wald = 0.05, $df = 1$, $p = 0.83$), or between old males paired with either young or old females (Wald = 0.11, $df = 1$, $p = 0.74$). Overall, pairs of old females and young males had significantly higher proportions of EPP than all the other combinations combined (Wald = 5.07, $df = 1$, $p = 0.024$).

There was no assortative mating with respect to age, as we found no difference between the number of males or females paired with a younger, older or similar aged partner in 2003 ($\chi^2 = 0.25$, $df = 1$, $N = 38$ pairs, $p = 0.62$). Males significantly increased in mass from one year to the next, while females did not (Table 2). Neither males nor females showed a change in the day the first egg was laid, clutch size, hatching success or their share of total provisioning to nestlings from 2002 to 2003 (Table 2). When comparing

Table 1. Multilevel GLM showing the effect of male and female age on the proportion of EPP in broods ($N = 45$ broods of 30 different pairs). The parameter estimates (\pm SE), Wald test statistic and level of significance are shown.

| Model terms | Estimate (SE) | Wald statistic | df | <i>p</i> |
|-----------------------|---------------|----------------|----|----------|
| Male age | 0.12 (1.09) | 0.012 | 1 | 0.91 |
| Female age | 3.32 (1.23) | 7.28 | 1 | 0.007 |
| Male age * female age | −3.58 (1.65) | 4.70 | 1 | 0.03 |

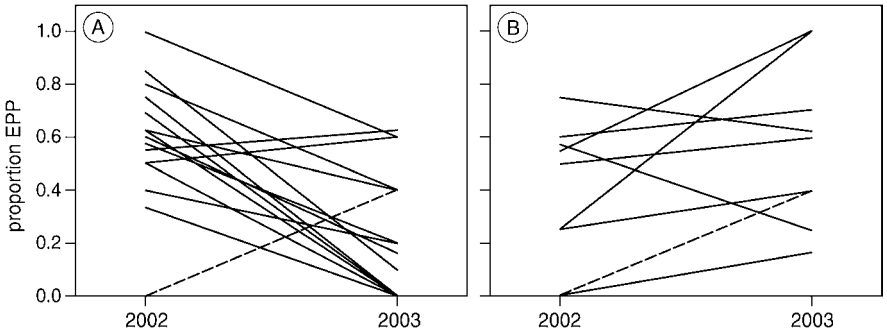


Figure 1. Proportion of EPP in broods produced in 2002 and 2003 by individual (a) male and (b) female reed buntings. Only one pair remained together in both years; the male and female of this pair are indicated by a dashed line. The proportion of EPP decreased for individual males (paired t -test; $t = 3.65$, $N = 15$, $p = 0.003$) and tended to increase for individual females ($t = -2.08$, $N = 9$, $p = 0.072$).

mass, first egg date, clutch size, hatching success, share of provisioning and fledging success between young and old individuals in 2003, we found no differences between the two age groups (all: $p > 0.17$).

The probability of males returning to our study site in 2003 was not affected by the proportion of EPP in their broods in 2002 (average proportion of EPP for resighted vs non-resighted males: 0.52 vs 0.60; $N = 66$ broods of 38 males; $\chi^2 = 1.13$, $df = 1$, $p = 0.29$). In contrast, females with a higher proportion of EPP in their broods in 2002, were less likely to return to our study site in 2003 (average proportion of EPP for resighted vs non-resighted females: 0.40 vs 0.66; $N = 60$ broods of 39 females; $\chi^2 = 6.73$, $df = 1$, $p = 0.01$). Females that returned tended to have shorter wings (i.e., were younger; 72.2 ± 0.65 mm, $N = 10$) than females that did not return (73.4 ± 0.38 mm, $N = 26$; $t = 1.68$, $df = 35$, $p = 0.10$).

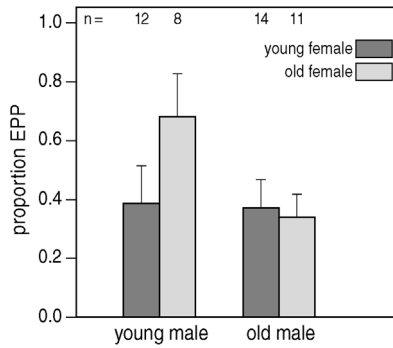


Figure 2. Proportion of EPP in reed bunting broods in relation to age of the pair members in 2003. Bars indicate mean + SE and sample sizes are shown above the bars.

Table 2. Comparison of quality measures (\pm SE) for individual male and female reed buntings between 2002 and 2003. Mass, first egg date (corrected for year effect), clutch size of first brood, hatching success (proportion of eggs hatched) and share of total provisioning within individuals from 2002 to 2003. Statistics for Wilcoxon signed-ranks tests are presented.

| | | N | 2002 | 2003 | z | p |
|----------|--------------------------|----|-----------------|-----------------|-------|-------|
| Males: | Mass (grams) | 15 | 19.2 \pm 0.2 | 19.5 \pm 0.2 | -2.45 | 0.014 |
| | 1 st egg date | 15 | -4.0 \pm 2.3 | -1.9 \pm 1.6 | -0.54 | 0.59 |
| | Clutch size | 15 | 4.9 \pm 0.1 | 4.9 \pm 0.1 | 0.0 | 1.0 |
| | Hatching success | 15 | 0.91 \pm 0.04 | 0.85 \pm 0.05 | -0.95 | 0.34 |
| | M/(M+F) provisioning | 13 | 0.37 \pm 0.04 | 0.32 \pm 0.04 | -0.94 | 0.35 |
| Females: | Mass (grams) | 8 | 18.0 \pm 0.4 | 18.6 \pm 0.3 | -1.54 | 0.12 |
| | 1 st egg date | 9 | 3.3 \pm 5.4 | -1.6 \pm 2.1 | -0.30 | 0.77 |
| | Clutch size | 9 | 5.0 \pm 0.2 | 5.0 \pm 0.0 | 0.0 | 1.0 |
| | Hatching success | 9 | 0.90 \pm 0.04 | 0.96 \pm 0.3 | -1.30 | 0.19 |
| | F/(M+F) provisioning | 5 | 0.61 \pm 0.07 | 0.59 \pm 0.03 | -0.67 | 0.50 |

Discussion

As expected following the higher total fertilisation success of older males (Bouwman et al., in press b), the proportion of EPP in their broods decreased with age for individual male reed buntings. This pattern was not due to higher return rates for high quality (i.e., less cuckolded) males than for low quality (i.e., more cuckolded) males, as we found no relation between the degree of cuckoldry in 2002 and the probability of a male's resighting in 2003. In

contrast to males, the level of EPP in the broods of females tended to increase with age.

The finding that females with high levels of EPP in their broods were less likely to return to our site, may be due to older females (with higher levels of EPP) being more likely to die as a consequence of ageing. This suggestion was supported to some extent, as females that did return tended to have shorter wings (i.e., were younger) than females that did not return. Following this reasoning males are also expected to suffer from an increased likelihood to die of ageing and thus should return less often than young males (i.e., males with high levels of EPP). This, however, is clearly not the case, since the probability of males returning was not affected by the levels of EPP in their nests. Alternatively, there may be differential costs of engaging in extra-pair mating behaviour to males and females. Disease transmittance as a potential cost of engaging in EPCs (Birkhead & Møller, 1992; Sheldon, 1993) is unlikely to explain the results, since it would (again) affect both old males and old females. Costs of EPCs that are higher or even solely present for females, however, may lead to lower return rates for females with high levels of EPP, either through lower survival or by moving to other breeding sites. Such costs could for instance consist of male harassment or a reduction in paternal care (Birkhead & Møller, 1992; but see Bouwman et al., 2005).

When comparing across individuals in 2003, we found that the proportions of EPP in broods did not only depend on the age of either the social male or female (although in the latter case the relationship was not significant), but also on the age of their social partner. We found that pairs consisting of young males and old females had higher levels of EPP in their broods compared to the other pair combinations. This pattern is similar to that found in coal tits (Dietrich et al., 2004), but to our knowledge has not been reported in any other species.

There are several possible explanations why older females have higher proportions of EPP in their brood than younger females. Firstly, extra-pair mating behaviour may be constrained by the conflict over parental investment and the need for paternal care ('constrained female hypothesis'; Westneat et al., 1990; Gowaty, 1996). If males reduce paternal care when the rate of cuckoldry increases, then only females that are capable of raising a brood alone or with reduced male assistance, for instance older females (Saether, 1990), can afford producing a high proportion of EPP in their brood. Several studies have reported a decline in paternal care with increasing cuckoldry

(Dixon et al., 1994; Sheldon & Ellegren, 1998; Lifjeld et al., 1998; Chuang-Dobbs et al., 2001), but others showed no relationship (e.g., Kempenaers et al., 1998; Peterson et al., 2001; Dickinson, 2003). However, this is unlikely to explain our results, because female reed buntings that produced a high proportion of extra-pair young did not suffer the cost of decreased paternal care in our population (Bouwman et al., 2005; but see Dixon et al. (1994) for the opposite result in a different population of reed buntings). Furthermore, older females did not feed offspring more in relation to their partner than younger females. We did not find any difference between old and young males in their share of parental care, suggesting that male parental effort does not change with age. Unfortunately, we were not able to determine whether the conflict over investment changed with age, i.e., whether male adjustment of parental care in relation to paternity differed between young and old males.

A second explanation for increased EPP with female age may be that males prefer attempting EPCs with older females, as older females may be of higher quality. However, mass, clutch size, hatching success and share in feeding rates within individual female reed buntings did not change between years and none of the measured variables, including fledging success, differed between age groups in 2003. With increase in age, females tended to increase in mass ($p = 0.12$), which is in the expected direction. In addition, the absolute difference in mass between years within individual females is also numerically twice as high as that of males. Since the sample size was small ($N = 8$), we cannot yet exclude that older females weigh more than young ones.

A third explanation for increased EPP with female age may be that older females become more choosy and make greater demands on the quality of the male that sires their offspring. Female mating preferences have been shown to change with age in satin bowerbirds (*Ptilonorhynchus violaceus*; Coleman et al., 2004) and guppies (*Poecilia reticulata*; Kodric-Brown & Nicoletto, 2001). Although we may expect that older females are better capable of choosing a high quality social partner and thus be less inclined to seek EPCS, we did not find any evidence for (dis)assortative pairing according to age (i.e., older female reed buntings are just as likely to pair up with young males as with old males). If older females do become more choosy, they may be more inclined to seek EPCs when paired to a young male. Alternatively, older females may become more experienced at escaping mate guarding behaviour of their partner, leading to more EPFs when a young male is paired to an old

female than to a young female. A study on a Norwegian population of reed buntings showed mate guarding by the social male to be effective, as it was negatively related to cuckoldry rate (Marthinsen et al., in press). However, our expectation that young males invest more in mate guarding was not supported in this Norwegian population, as there was no difference in the time that old and young males spent mate guarding (Marthinsen et al., in press). Unfortunately, we did not measure mate guarding behaviour in our population, so we could not determine if mate guarding intensity changed with age. Older females having fewer extra-pair young in their brood when paired with old males may be explained either by females choosing not to mate outside the pairbond or by older males being more successful at guarding their females. Detailed behavioural observations would be required to distinguish between these two possibilities.

Our results emphasize that not only male age, but also female age and their interaction is potentially a very important aspect to understanding extra-pair mating behaviour. This pattern of partner age and proportions of EPP has now been revealed in two species (Dietrich et al., 2004; this study), and may be quite general across avian species. Furthermore, as suggested by Westneat & Stewart (2003), it is clear that detailed behavioural observations are needed to understand how male-female interactions during the breeding season influence the occurrence and extent of extra-pair mating and the likelihood of cuckoldry.

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